# AGGREGATION AND PREDATOR AVOIDANCE IN WHIRLIGIG BEETLES (COLEOPTERA: GYRINIDAE)

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*Abstract.* — Whirligig beetles (Coleoptera: Family Gyrinidae) aggregate on the surface of ponds, lakes, and streams. This study examines how these aggregations protect the beetles from predation. The more beetles in an aggregation, the more quickly the group as a whole responds to the approach of stimuli. Experiments indicate that individual beetles either sight a stimulus themselves, or respond to waves generated by fleeing conspecifics. The distance between two beetles is important in determining how quickly a blinded beetle reacts to wave cues. Two hypotheses can explain the warning mechanism used by aggregations. (1) A high contact rate between aggregation members leads to increased physiological arousal which allows more rapid individual response, or (2) Environmental scanning is enhanced with the addition of more eyes to the group. Evidence from laboratory experiments supports the latter explanation.

Whirligig beetles (Coleoptera: Family Gyrinidae) live in an exposed habitat: the water surface of ponds, lakes, and streams, where they aggregate in large rafts, sometimes in multi-species groups. Rafts of 20,000 individuals have been reported (Heinrich and Vogt, 1980). Beetles remain in these rafts all day, dispersing at dusk to forage singly. Most rafts appear to occur in the same location day after day, but individual beetles move around from one raft to another without apparent pattern (Heinrich and Vogt, 1980). Although highly conspicuous, gyrinids are not common prey of aquatic vertebrate predators (Benfield, 1972). In this paper, we examine the role of gyrinid aggregation in predator avoidance.

Several hypotheses have been offered for this aggregating behavior. Brown and Hatch (1929) suggest it to be an orientation behavior due to habituation to certain visual patterns in the environment. On the other hand, Benfield (1972) and Heinrich and Vogt (1980) suggest a defensive function for gyrinid aggregations. Gyrinid beetles exude a strong-smelling secretion from the pygidial glands believed to be a defensive substance (Benfield, 1972; Meinwald et al., 1972; Miller et al., 1975; Newhart and Mumma, 1978; Heinrich and Vogt, 1980; Dettner, 1985). To demonstrate the noxious quality of the substance, Benfield (1972) fed gyrinids to fish and found (after a number of trials) that the fish rejected the beetles on sight. He hypothesized that the aggregations serve to advertise the gyrinids' unpalatability. Heinrich and Vogt (1980) suggested that the groups occur in areas where there are no predators or where the predators have already learned to avoid the beetles.

Defense appears to be the main function of these aggregations. Interactions among

individual beetles appear limited to maintaining interindividual distance, or sexual signaling (Kolmes, 1983a; see also Freilich, 1986), which excludes sociality as the function of the aggregations. The groups are not mating swarms, because aggregations occur throughout the months the adults are active, and not just during the mating season (Istock, 1967). In addition, pond-dwelling gyrinids disperse at night to forage singly (Heinrich and Vogt, 1980; but see Kolmes, 1983b; Vulinec and Kolmes, 1987), suggesting that the rafts do not function in foraging.

This study examines how gyrinid beetle aggregations function in predator avoidance by providing an early warning of predator approach. We first examined whether aggregation does allow an early warning of predator approach (group effect). We also determined the mechanism of information transfer among aggregation members. Finally, we tested two competing hypotheses that explain how early warning is accomplished: (1) Beetles in large groups are more physiologically aroused, or (2) Beetles in large groups have more eyes available to scan the environment.

### MATERIALS AND METHODS

*Group effect.* We performed a field experiment to test the effect of group size on group avoidance response. A human was used as a predator stimulus in this experiment to insure constant approach speed. One of us approached different-sized groups of gyrinids that were aggregated on ponds. Speed of approach was approximately constant at 150 cm/s. A point in the middle of the group was noted by an observer viewing through a Super-8 tripod-mounted camera. Measurement could then be made from this point to the location of the experimenter at the time that the entire group's defensive movements began. Defensive movements can be easily distinguished from random swimming and the group reacts almost instantaneously. We obtained group sizes from the Super-8 film viewed with a stop-action projector. Thirty-five different groups were tested over a 4-day period. A regression was performed between reaction speed and group size and the best fit line was obtained by the least squares method. A *t*-test was performed to determine the significance of the slope.

*Information transfer.* We used temporarily blinded beetles to determine if beetles need to see the stimulus to react, and if the proportion of sighted beetles in a group is important to the speed of group reaction. Beetles were blinded by placing them in a foil-lined finger bowl and exposing them to a 150-watt photoflood lamp for 10 minutes (Kolmes, 1983b). We considered the beetle blinded if it did not react to a hand waved over it. Blinding was effective for 10 to 15 minutes after treatment and no experiments were run for longer than five minutes with the same beetles. In the first experiment, a varying proportion of 20 beetles was blinded. They were all placed in a large white porcelain testing arena (115 cm × 54 cm × 30 cm depth), which allowed good visibility; water level was maintained at 10 cm and temperature at 15°C. A predator stimulus (human hand) was shown from above and we recorded the time (up to a maximum of 60 seconds) at which all beetles in the group began moving defensively. Beetles were not reused, so the sample sizes of the groups were necessarily small.

We conducted a laboratory experiment to examine the effect of a disturbed beetle's proximity on the reaction speed of another. The initial distance between the two beetles was delimited by using three sizes of finger bowls (100, 200, or 300 mm in diameter) filled with 2 cm of 15°C water. The blinded beetle was placed in a bowl

and allowed approximately 3 minutes to acclimate, until it came to rest near the side of the bowl; the sighted beetle was then placed in the finger bowl at the farthest point from the blinded beetle. The sighted beetle immediately began defensive swimming: a rapid zig-zag movement very different from non-defensive swimming. This allowed us to record the time between the release of the sighted beetle and the initiation of defensive swimming by the blinded beetle. If the beetles made physical contact before the blinded beetle began defensive movements, or if the sighted beetle dove under the water, the trial was excluded. This experiment was conducted seven times for each size finger bowl, with different beetles each time. Data were analysed using a one-way analysis of variance.

Chemical cues, in addition to tactile ones, might be used by gyrinid beetles to gain an early warning of danger. To determine if pygidial gland secretions are used in this context, we performed two tests: (1) A beetle's secretion was milked from the pygidial glands onto a cotton swab. This secretion, mostly norsesquiterpene (Miller et al., 1975), is normally released whenever a beetle is held. The swab was carefully dipped into the water of an artificial pool near an aggregation of five beetles. We repeated this procedure with five different beetles and five different groups. (2) A beetle was held and squeezed to release its secretion, and the tip of its abdomen was placed in the water near an aggregation of five beetles. This trial was repeated five times with different beetles each time.

We used only above water stimuli to invoke defensive swimming. We attempted to simulate underwater predation by moving a predator model (plastic fish) beneath a suspended glass bowl containing beetles. We got no response from any beetle even when the model was backlit.

*Hypothesis 1: increased physiological arousal.* All beetles (*Dineutes hornii* Roberts 1895) used in the laboratory studies were collected with a dip net from five different sites in southwestern Ohio between August 1980 and June 1983. These beetles were placed into plastic quart containers half-filled with water, then kept in aquaria in the lab. Care was taken to disturb or handle them as little as possible.

We performed a laboratory experiment to examine the hypothesis of physiological arousal. In the first experiment, we placed beetles of three different group sizes (1, 10, 20) in the water-filled testing arena and allowed them one hour to acclimate. A predator stimulus (in this case, the senior author) was shown from above. We recorded the time from the initiation of the stimulus to the defensive reaction of one beetle by timing the first beetle sighted on looking into the arena. Direction of sight was shifted to a different part of the arena for the beginning of every trial, which effectively randomized the trials. Because these beetles perform specific swimming movements in response to novel or sudden stimuli, we obtained accurate response times with a 0.1 second stop watch. Each group size was tested 20 times with beetles randomly drawn from a common pool of 73 beetles. Data were analysed by a one-way analysis of variance.

*Hypothesis 2: environmental scanning.* To determine if the beetles' reaction speed is independent of the speed of a predator's approach, we placed six beetles in a 20 cm diameter finger bowl that was half-filled with water. A predator stimulus (a black paper square 3 cm × 3 cm attached to a string) was lowered from a height of 90 cm toward the beetles at three different speeds, approximately 23 cm/s, 40 cm/s, and 77 cm/s. We then measured the distance of the black square from the beetles when all
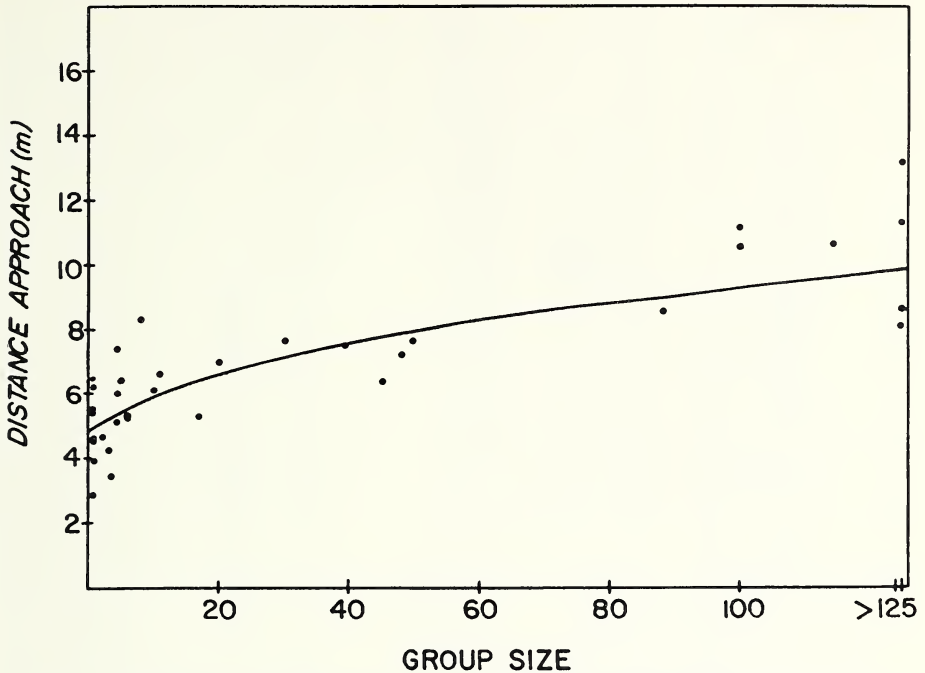
Fig. 1. Distance (m) a predator stimulus could approach a group of gyrinids before elicting a defensive response as a function of group size. Line is fitted by eye.

six had begun defensive movements (which occurred within milliseconds of one another). All three approach speeds were tested 12 times with new beetles each time. Data were analysed by a one-way analysis of variance.

### RESULTS

*Group effect.* When different-sized groups of gyrinids were approached by a human (with a constant approach speed), the reaction speed of the whole group (i.e., until the last beetle reacted) varied with group size (Fig. 1). Larger groups reacted significantly faster to a predator stimulus than smaller groups ($t = 7.5$, df $= 32$, $P < 0.001$, based on a linear regression [y = 0.031x + 5.48; $r = 0.798$]).

*Information transfer.* Twenty beetles in a group with 0% or 10% blinded all reacted very quickly to a predator stimulus. When a greater percentage of beetles were blinded (25%–50%), reaction speed was much more variable; however, in all trials, every beetle in the group reacted with defensive swimming before 60 seconds had elapsed. When 75% or more were blinded, entire group reaction did not occur within the 60-second limit (Fig. 2).

The size of the arena, and so presumably the distance between two beetles, is important in determining the speed of reaction (Fig. 3). The farther away a beetle is initially from its blinded neighbor, the longer it will take that neighbor to react ($F = 24$, df $= 2$ and 18, $P < 0.01$, ANOVA).
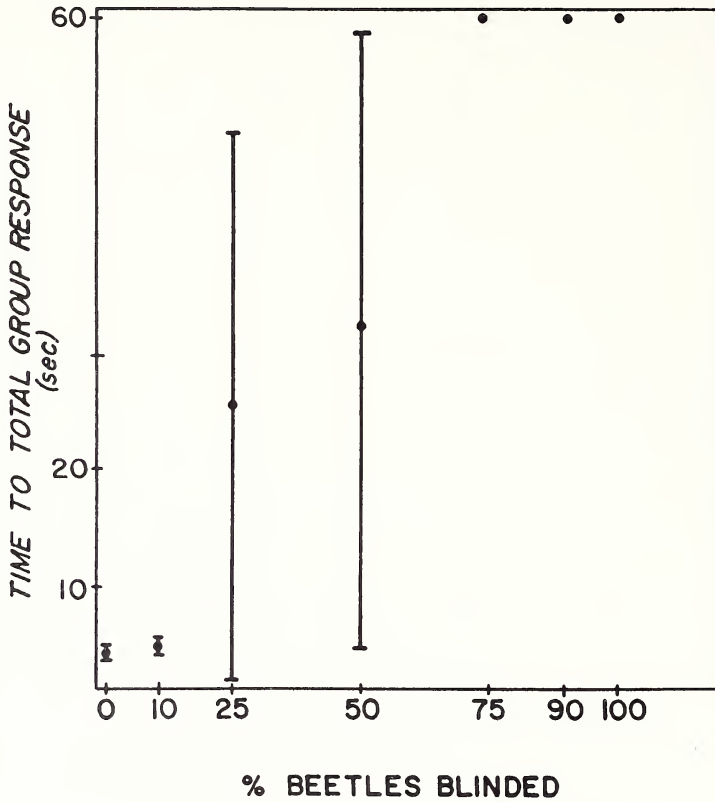
**% BEETLES BLINDED**

Fig. 2.   Response time (s) of twenty beetles as a function of the proportion of blinded beetles. Error bars include ±1 standard error. The N for each treatment is as follows: 0% = 13, 10% = 2, 25% = 5, 50% = 5, 75% = 2, 90% = 2, 100% = 2. Response time of all treatments with 75% or more beetles blinded was actually greater than 60 seconds; however, the observation period was terminated at that time.

No beetle showed any reaction to the pygidial gland secretion either on a cotton swab or from the abdomen of a conspecific.

*Hypothesis 1: increased physiological arousal.* Individual beetles from larger groups do not react faster than those in small groups (F = 0.9, df = 2 and 57, NS, ANOVA). Mean response times are 1.4 second, 1.5 second, and 0.9 second, for beetle group sizes of 1, 10, and 20.

*Hypothesis 2: environmental scanning.* The beetles' reactive distance varied inversely with the approach speed of the predator stimulus (F = 21.43, df = 2 and 33, $P < 0.001$, ANOVA). Mean distances are 21.5 cm, 16.8 cm, and 8.2 cm respectively, for model speed of approach of 23 cm/s, 40 cm/s, and 77 cm/s.

### DISCUSSION

*Group effect and information transfer.* Our field experiment demonstated that large groups of gyrinids are better able to avoid predators than small groups or single
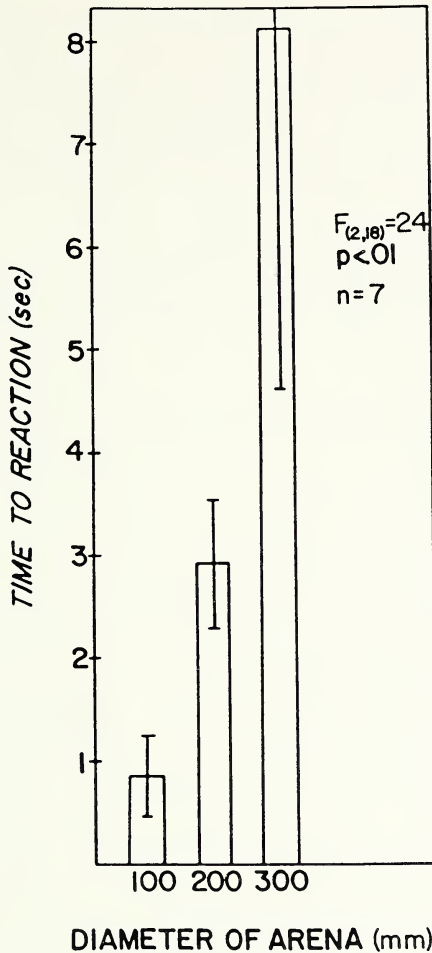
Fig. 3. Response time (s) of a blinded beetle to defensive swimming of an intact beetle as a function of the diameter (mm) of the arena (initial distance between the two). Error bars include ±1 standard error.

individuals, as anyone who has tried to collect gyrinids with a dip net can verify. Experiments with the blinded beetles indicate that beetles react to the defensive movements of other beetles even when they cannot see the stimulus themselves. These beetles are reacting only to surface waves propagated by the defensive swimming reactions of the sighted beetles. In order to react with defensive swimming, a beetle must feel a neighbor's waves from within a certain distance, an effect that may be due to wave attenuation, which occurs at distances of more than six body lengths (Tucker, 1969). When 0 to 10% of the group were blinded, the reaction speed of the entire group was less than 5 seconds, however, total group response was quite variable when 25% to 50% of the group were blinded. This result may indicate that there is

a threshold level for reaction to visually perceived stimuli that is lower than that for tactile stimuli. A response threshold in gyrinids may be a means of energy conservation. Alternatively, a large variance in interindividual distance within a partially blinded aggregation will result in a large variance in response time, due to the relatively slow speed of waves on the water surface. If response thresholds are to be demonstrated to mediate gyrinid escape behavior, this artifact must be experimentally or statistically factored out, a procedure that was beyond the scope of the present study.

The distance between beetles is important in determining a beetle's reaction speed, which suggests that a close aggregation may well be adaptive in transmitting predator defense information. Interindividual distance of aggregation members rarely exceeds 7 cm (Vulinec and Kolmes, 1987), the upper limit of wave propagation (Tucker, 1969).

Because blinded beetles reacted to wave motion, we infer that tactile cues are very important in the defensive response of gyrinids, but that visual perception of a neighbor's defensive swimming is not. Although gyrinids react quickly to perceived visual stimuli above the water surface, the function of the lower eyes is undetermined. Spectral sensitivity and electrophysiological studies of gyrinids reveal little difference between the two pairs of eyes (Carthy and Goodman, 1964; Bennett, 1967). Anatomical studies on the lower eye (Carthy and Goodman, 1964) do not indicate that it is adapted for sight under water, and our attempts to simulate the approach of a predator under the water surface elicited no reaction. A possibility is that the lower eyes are used during flight (D. Fong, pers. comm.). We also found that the pygidial gland secretion elicits no defensive response from a group of beetles. Defensive behavior occurred only in response to visual stimuli, or another beetle's wave motion.

*Hypothesis 1: increased physiological arousal.* In our experiments, individual beetles in large groups did not react any faster to stimuli than those in small groups or those that were solitary. This result indicates that beetles in larger groups are not more physiologically aroused than single beetles. Furthermore, pond gyrinids in aggregations contact each other at relatively low frequencies; less than 0.5 per minute (Vulinec and Kolmes, 1987). This low contact rate is unlikely to result in increased arousal. Contacts between individuals are also non-random (Freilich, 1986; see also Foster and Treherne, 1982), a behavior incompatible with a hypothesis of physiological arousal.

*Hypothesis 2: environmental scanning.* Pulliam's model (1973) explains why birds may aggregate in large numbers while foraging. According to this model, the reaction speed of all individuals to a predator is faster in large groups than in small because, in a large group, more eyes are available to scan the environment; therefore predators will be detected sooner. There are a number of empirical studies that support this hypothesis. Powell (1974) demonstrated that birds in flocks spend less time individually in surveillance, but are able to detect a predator sooner than single birds. Similarly, Kenward (1978) found that a trained goshawk's attacks on groups of pigeons became less successful the larger the group size. Sticklebacks actively pursue stray *Daphnia* in preference to a school (Milinski, 1977a, b), and predators such as squid, cuttlefish, pike, and perch experienced lowered success in capture the larger the group size of prey fish (Neill and Cullen, 1974).

Our data demonstrate that large groups of gyrinids respond to a predator stimulus

more quickly than small groups. Because this finding also supports the physiological arousal hypothesis, we needed to show that the speed of the beetles' response varied with the speed of predator approach. If a group's response time to a stimulus is independent of the approach speed of that stimulus, and is based instead on intrinsic factors, there should be no difference in the time of response (reactive distance) of a group of five insects to a stimulus that moves toward them at different speeds (Treherne and Foster, 1980). Since we found that the reactive distance of the beetles varied inversely with the stimulus approach speed, and that individual beetles in large groups did not react more quickly than solitary beetles, we suggest that environmental scanning and not physiological arousal is responsible for the decreased response time in larger groups. Additionally, insects that rely on environmental scanning for early warning of danger will react quickly if they happen to see the danger themselves. Thus, there should be a great deal of variability in the response time of solitary insects, depending on whether they see the stimulus or not. However, in the fastest cases, a solitary insect should react as quickly as a group. In fact, Figure 1 shows that the fastest solitary insect responds as quickly to a stimulus as beetles in groups up to about 50 members.

Predatory success on prey groups may be influenced by three factors: the dilution effect, increased detection capabilities of the prey, and the increased confusion of predators by many rapidly moving prey (Bertram, 1978). There is evidence that individuals in a group are protected just by being surrounded by conspecifics. For example, Foster and Treherne (1981) showed that fish attacks per individual *Halobates robustus* declined with increasing group size, an effect that is independent of any avoidance behaviors of the prey. The zig-zag swimming motion of whirligig beetles may serve to confuse predators. Additionally, these beetles swim extremely fast, with bursts up to 144 cm/s (Vulinec, 1987), a speed that approaches the burst swimming speed of possible fish predators (approximately 200 cm/s; Lagler et al., 1977). It seems likely that all three factors are important to whirligig beetle defense, with increased detection capabilities the front-line defense. The difference between vertebrate prey groups and these aquatic insects in their use of this defense is the use of substrate vibrational cues of danger, rather than visual or auditory ones. Tucker (1969) suggested that beetles use their own waves to echolocate, and Kolmes (1983b) found that beetles located prey by surface waves. Surface vibrational cues may also be used in precopulatory communication (Kolmes, 1985). Our data indicate that waves on the surface are also used as an early warning system. The transmission of the impulse would spread rapidly through the group, on an order similar to the "Trafalgar effect" observed in *Halobates robustus* by Treherne and Foster (1981), although without the necessity of actual contact between insects. The mean responsive distance of gyrinid groups in the field reaches an apparent asymptote above 60 to 80 individuals. This plateau indicates an upper limit beyond which adding more individuals does not contribute to increased detection capabilities for group members, and may explain why huge rafts of gyrinids are often divided into units of 50 to 100 individuals (Heinrich and Vogt, 1980).

The pygidial secretion may play a significant role in whirligig beetle defense (Benfield, 1972; Heinrich and Vogt, 1980). It is not known if the secretion is released into the water during escape and prior to capture. This possibility needs to be investigated before pooling of defensive secretions can be proposed as an explanation

of gyrinid aggregations. Alternatively, early release of the secretion may assist the beetles' movement across the water surface (Vulinec, 1987). Our data suggest that gyrinid beetles have an effective pre-attack defense. The pygidial substance may be used as a last resort defense, after the beetle has actually been captured.

The hypothesis of environmental scanning is an extension of Hamilton's selfish herd hypothesis (Hamilton, 1971). Grouping benefits the individual, both by decreasing its chances of being singled out by a predator, and by increasing the number of eyes available to watch for a predator. Thus, a group can detect a predator sooner than a single individual. This tactic is especially effective for an animal in an exposed habitat such as the surface of a pond. The benefits of aggregation to gyrinid beetles are further enhanced by their ability to detect a neighbor's defensive movements and react accordingly, whether or not they have sighted the stimulus themselves.

Fossil gyrinid morphology (Hatch, 1927) suggests that gyrinid beetles were generalized swimmers before they were surface swimmers. Because many other aquatic beetles and many terrestrial Adephaga possess chemical defenses and pygidial gland secretions (Blum, 1981; Dettner, 1985), we suggest that the chemical defense was present before water surface living evolved. Therefore, the following scenario is proposed for the evolution of gyrinid defenses: terrestrial existence → chemical defense → aquatic existence → exploitation of the water surface → aggregation as the primary defense in response to the exposed habitat.

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